Main prey and predators and estimates of mortality of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s

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Main prey and predators and estimates of mortality of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s

by

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TABLE OF CONTENTS

Page

LIST OF TABLES iv
LIST OF FIGURES iv
ABSTRACT v
RÉSUMÉ vi
INTRODUCTION 1
MATERIAL AND METHODS 2
Data used in modelling 2
Inverse modelling 2
Cod background 4
RESULTS 8
Main prey groups consumed by small (< 35 cm) cod 8
Main prey groups consumed by large (> 35 cm) cod 9
Role played by cod in the northern Gulf ecosystem 9
Main mortality causes on small (< 35 cm) cod 10
Main mortality causes on large (> 35 cm) cod 10
DISCUSSION 11
CONCLUSION 13
ACKNOWLEDGMENTS 14
REFERENCES 15

LIST OF TABLES

Table 1. Functional groups used in modelling in the northern Gulf of St. Lawrence for each time period....18

Table 2. Mean, minimum, and maximum values for small cod used in inverse modelling for each time period....21

Table 3. Mean, minimum, and maximum values for large cod used in inverse modelling for each time period....22

Table 4. Diet composition of small cod used in modelling for each time period....23

Table 5. Diet composition of large cod used in modelling for each time period....24

LIST OF FIGURES

Figure 1. Gulf of St. Lawrence map showing NAFO divisions 4R, 4S, and 3Pn, which constitute the management unit for the northern Gulf of St. Lawrence cod....25

Figure 2. Historical catches and total allowable catch for 4RS3Pn cod....26

Figure 3. Prey consumed by small (< 35 cm) cod estimated for each time period....27

Figure 4. Prey consumed by large (> 35 cm) cod estimated for each time period....28

Figure 5. Predation mortality on fish by different groups showing the main predators in the northern Gulf for each time period....29

Figure 6. Main mortality causes (predation and natural mortality other than predation; i.e., other causes) for small (< 35 cm) cod estimated for each time period....30

Figure 7. Main mortality causes (fishing, predation, and natural mortality other than predation; i.e., other causes) for large (> 35 cm) cod estimated for each time period....31

Figure 8. (a) Cod spawning stock biomass (mature; SSB) and total biomass (age 3+) and (b) recruitment rate (age 3 biomass/SSB) by year....32

ABSTRACT

Savenkoff, C., M. Castonguay, D. Chabot, A. Fréchet, M. O. Hammill, and L. Morissette. 2006. Main prey and predators and estimates of mortality of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2666: vi+32 pp.

We used results of mass-balance models to describe the changes in the structure and functioning of the northern Gulf of St. Lawrence ecosystem related to Atlantic cod (*Gadus morhua*) for the mid-1980s, the mid-1990s, and the early 2000s. The net decrease in biomass of the demersal species in the early 1990s and the ensuing drop in predation led to an ecosystem structure dominated by small-bodied pelagic species and marine mammals. Cod (both small and large) consumption largely decreased from the mid-1980s to the mid-1990s. Large zooplankton, shrimp (mainly *Pandalus borealis*), capelin (*Mallotus villosus*), and small planktivorous pelagics (mainly Atlantic herring *Clupea harengus*) were among the main prey consumed by small cod for each time period. The proportion of fish in the diet of large cod decreased from 77% in the mid-1980s, when they mainly consumed capelin, to 49% in the early 2000s. In the early 2000s, the main prey of large cod were large zooplankton and shrimp. There was a net decrease in total mortality and predation on small and large cod from the mid-1980s to the mid-1990s. Fishing mortality on large cod also decreased over the same time period (moratorium). From the mid-1990s to the early 2000s, the biomass of both small and large cod doubled. Predation on small cod increased slightly over the same time period while predation on large cod was similar. However, the most noticeable increase in mortality on large cod from the mid-1990s to early 2000s came from fishing, which increased by a factor of 23. Cannibalism also appeared to be a non-negligible source of mortality on cod. A high proportion (between 30 and 40%) of the total mortality of large cod could not be explained by either fishing or predation for each period (i.e., other mortality causes). This suggests that other processes in the ecosystem were not accounted for in the models.

RÉSUMÉ

Savenkoff, C., M. Castonguay, D. Chabot, A. Fréchet, M. O. Hammill, and L. Morissette. 2006. Main prey and predators and estimates of mortality of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2666: vi+32 pp.

Nous avons utilisé les résultats de modèles d'équilibre de masse pour décrire les changements dans la structure et le fonctionnement de l'écosystème du nord du Golfe du Saint-Laurent associés au stock de morue franche (*Gadus morhua*) pour le milieu des années 1980, le milieu des années 1990 et le début des années 2000. La forte diminution des biomasses des espèces démersales au début des années 1990 et la chute résultante de leur pression de prédation ont conduit à une structure de l'écosystème dominée par des petits poissons pélagiques et des mammifères marins. Il y a eu une forte diminution de la mortalité totale et de la prédation sur la petite et la grande morue depuis le milieu des années 1980 jusqu'au milieu des années 1990. La consommation de la morue (à la fois la petite et la grande) a largement diminué depuis le milieu des années 1980 jusqu'au milieu des années 1990. Le grand zooplancton, les crevettes (surtout *Pandalus borealis*), le capelan (*Mallotus villosus*) et les petits pélagiques planctivores (principalement le hareng d'Atlantique *Clupea harengus*) étaient parmi les principales proies consommées par la petite morue à chaque période de temps. La proportion de poissons dans l'alimentation de la grande morue a diminué de 77 % au milieu des années 1980, période où elle consommait surtout du capelan, à 49 % au début des années 2000. Au début des années 2000, les principales proies de la grande morue étaient le grand zooplancton et les crevettes. La mortalité de la grande morue par la pêche a également diminué pendant la même période de temps (moratoire). Depuis le milieu des années 1990 jusqu'au début des années 2000, la biomasse à la fois de la petite et la grande morue a doublé. La prédation sur la petite morue a légèrement augmenté alors que la prédation sur la grande morue est restée identique. Toutefois, l'augmentation de mortalité la plus importante pour la grande morue est venue de la pêche qui a augmenté d'un facteur 23 depuis le milieu des années 1980 jusqu'au début des années 2000. Le cannibalisme apparaissait également comme une source non négligeable de mortalité de la morue. Une forte proportion (entre 30 et 40 %) de la mortalité totale de la grande morue n'a pu être attribuée ni à la pêche, ni à la prédation à chaque période (autres causes de mortalité). Cela suggère que des processus dans l'écosystème n'ont pas été comptabilisés dans les modèles.

INTRODUCTION

Abundance of many Atlantic cod (*Gadus morhua*) and groundfish stocks in the Northwest Atlantic declined to low levels in the early 1990s, resulting in the cessation of directed fishing for these stocks (CAFSAC 1994, Swain and Castonguay 2000, Gascon 2003). In the northern Gulf (Northwest Atlantic Fisheries Organization [NAFO] divisions 4RS; Figure 1), dramatic declines in the biomass of the large-bodied demersal predators such as Atlantic cod (15 fold), redfish (*Sebastes* spp.; 8 fold), and large demersals (including white hake *Urophycis tenuis*, black dogfish *Centroscyllium fabricii*, and Atlantic halibut *Hippoglossus hippoglossus*; 4 fold) occurred from the mid-1980s to the mid-1990s (Morissette et al. 2003, Savenkoff et al. 2004a). Some authors argued that the sole reason for the collapse was overfishing (Hutchings and Myers 1994, Myers et al. 1996), while others proposed that a natural shift to less favourable environmental conditions also made stocks more vulnerable to fishing through processes such as an earlier migration to wintering grounds that shortened the feeding season (Castonguay et al. 1999). Others noted declines in condition (Lambert and Dutil 1997) as well as in growth and production (Dutil et al. 1999) and an increase in natural mortality (DeYoung and Rose 1993, Dutil and Lambert 2000).

The changes in the northern Gulf ecosystem were also accompanied by a decrease in total catches and a transition in landings from long-lived, piscivorous groundfish toward planktivorous pelagic fish and invertebrates (Savenkoff et al. submitted[1]). This trend in fishing down the food web has unfortunately become widespread in fisheries throughout the northern hemisphere (Pauly et al. 1998). There was a near 4-fold decrease in total catches from the mid-1980s to mid-1990s (from 1.83 to 0.48 t km^{-2} yr^{-1}). This decrease was entirely due to the near disappearance of catches of demersal species. Reported cod and redfish landings were 1.11 and 0.26 t km^{-2} yr^{-1} (62% and 14%, respectively, of the total catches) during the mid-1980s while forage fish and invertebrates represented 0.21 and 0.14 t km^{-2} yr^{-1} (12% and 8%, respectively). During the mid-1990s, cod and redfish landings accounted for 0.003 and 0.02 t km^{-2} yr^{-1} (only 1% and 4%, respectively, of the total catches) while catches of forage fish and invertebrates represented 0.20 and 0.23 t km^{-2} yr^{-1} (43% and 48%, respectively). In the early 2000s, a few years after a limited cod fishery had resumed in the northern Gulf, cod catches increased to 0.07 t km^{-2} yr^{-1} (11% of the total catches) while redfish landings accounted for 0.01 t km^{-2} yr^{-1} (1% only; moratorium period). The remaining fisheries showed only minor changes: catches of forage fish and invertebrates represented 0.23 and 0.32 t km^{-2} yr^{-1} (35% and 49%, respectively).

Mass-balance models, using inverse methodology, have been constructed for the northern Gulf of St. Lawrence ecosystem for the mid-1980s, the mid-1990s, and the early 2000s to describe ecosystem structure, trophic interactions among groups, and the effects of fishing and predation on the ecosystem for each time period (Savenkoff et al. 2004b, submitted[1]). In the mid-1980s, groundfish stocks were considered healthy and were fished. The situation was very different in the mid-1990s: most large-bodied demersal fish had declined severely from the previous period and many stocks were protected by moratoria on direct fishing. The last time period covers the early 2000s, the period after the moratoria for cod were ended and fishing had resumed, albeit at very low levels compared to historic levels (Fréchet et al. 2003). During that time, directed fisheries resumed even though demersal stocks showed no signs of recovery in the northern Gulf and in most other areas (Rice and Rivard 2003).

[1]: Savenkoff, C., Castonguay, M., Chabot, D., Bourdages, H., Morissette, L., and Hammill, M. O. Changes in the northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift? Submitted for publication.

In this report, we used results of mass-balance models to describe the changes in the structure and functioning of the northern Gulf of St. Lawrence ecosystem related to cod for the mid-1980s, the mid-1990s, and the early 2000s. Our results enable us to present the main prey and predators of juvenile and adult cods and to evaluate the effects of the major mortality causes (fishing, predation, and natural mortality other than predation) on cod for each time period.

MATERIAL AND METHODS

Data used in modelling

The data set covers a region of the northern Gulf of St. Lawrence (NAFO division 4RS) equivalent to a total area of 103,812 km^2 (Figure 1). The St. Lawrence Estuary was not included in the study. The nearshore region (depths < 37 m) was also excluded in the models, along with infra-littoral species such as American lobster (*Homarus americanus*), because this zone was not sampled by the research vessel survey and because exchanges between infra-littoral and mid- to off-shore zones are still poorly understood.

The periods covered by this analysis are the mid-1980s (1985–1987), before the collapse of groundfish stocks in most areas of the Northwest Atlantic, the mid-1990s (1994–1996), after the collapse of groundfish stocks, and the early 2000s (2000–2002), a few years after a limited cod fishery had resumed in the northern Gulf. The groundfish biomass was relatively stable at each time period covered by this analysis, even though the groundfish biomass varied between them (the coefficient of variation among years for biomass was between 29% and 31% for small cod, 3% and 21% for large cod, 12% and 43% for redfish, 26% and 47% for small Greenland halibut *Reinhardtius hippoglossoides*, and 7% and 47% for large Greenland halibut).

Based on data availability and the ecological and commercial significance of the species, the whole-system model of the northern Gulf of St. Lawrence was divided into different functional groups or compartments (32 for the mid-1980s and mid-1990s, 31 for the early 2000s) representing the main pelagic, demersal, and benthic species present (Table 1). The model structure for the early 2000s differs slightly from that of the mid-1980s and mid-1990s to incorporate ecological refinements (Savenkoff et al. 2005; Table 1). Details of the methods and data for the parameter estimates for each group as well as the modelling structure are given in Morissette et al. (2003) for the mid-1980s, Savenkoff et al. (2004a) for the mid-1990s, and Savenkoff et al. (2005) for the early 2000s. These three technical reports are available online at www.osl.gc.ca/cdeena/en/publications.shtml. In the "Cod background" section below, we present the details of the input data for cod only.

Inverse modelling

Inverse analysis is increasingly used in ecosystem modelling to compensate for the insufficiency of data on the ecosystem, to objectively reconstruct a large number of unknown flows or interactions from a small number of observations, and to generate a "snapshot" of the system at one moment in time (Vézina and Platt 1988, Savenkoff et al. 2004b, Vézina et al. 2004). As opposed to traditional approaches, the ecosystem is considered as a whole, taking into account trophic interactions between all functional groups.

Ecosystem inverse modelling is based on combining compartmental mass balance equations with data equations and eco-physiological constraints on the flows. The mass balance equations specify that, for each compartment, the sum of inflows (consumption for each consumer group) is balanced by the sum of outflows (production, respiration, and egestion for each consumer group), a net change in the biomass variable (ΔBi), and a residual term (ε). Here, we assumed that there was no change in biomass ($\Delta Bi = 0$) during each studied time period and that net migration was zero (migration out of or into the study area, food intake of predators that are not part of the system, etc.) (steady-state assumption). The equations calculated for this study were not exactly balanced, that is, the sum of the inputs and outputs for each compartment did not necessarily equal zero. These differences, termed the residuals, are represented by the residual term ε. The residual for each compartmental mass-balance, if it is not equal to zero, corresponds to an annual change in the biomass (ε/ biomass). Inverse modelling could thus find a solution that was not necessarily balanced (not in steady state).

Production was equal to the biomass lost to fishing, predation, and natural mortality other than predation (hereafter termed "other mortality causes"). Other mortality causes could include other natural causes of death such as disease or could reflect unsuspected processes occurring in the ecosystem, such as misreported catch (e.g., Savenkoff et al. 2004b), unsuspected migration, or other processes not accounted for in the model. For phytoplankton, the net (corrected for respiration) production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus were assumed to respire. Details of the model structure and method of solution for the different equations are given in Savenkoff et al. (2004b and submitted).

The models are useful in constraining observations into coherent pictures (Savenkoff et al. 2004b and submitted); however, since the number of flows to be solved exceeds the number of independent mass balance relations (i.e., an underdetermined system), there is no unique solution to any model. Also, it remains that the results are sensitive to some choices we made regarding the modelling structure and that other valid solutions are possible. However, for each model presented in the next section, the final solution is always the mean of 30 iterations with random perturbations of the input data (to a maximum of their standard deviations) and one solution without perturbation (the "initial solution") to provide an overall view of the ecosystem and to identify robust patterns. The estimated flows fell inside our *a priori* constraints and therefore represented a reasonable "middle ground" description. Simulated inverse analyses have shown that the general flow structure of ecosystems can be recovered with these techniques, although the details can be inaccurate (Vézina and Pahlow 2003).

Cod background

The northern Gulf cod stock overwinters in the deep waters off southwestern Newfoundland and then returns to the Gulf, moving northwards off Newfoundland's west coast (NAFO division 4R). Spawning takes place mainly during April and May in Esquiman Channel. During summer, the population migrates to the warmer coastal waters of Québec's lower North Shore and the west coast of Newfoundland.

Commercial landings increased considerably during the late 1950s and 1960s, but the stock declined to low levels by the mid to late 1970s. Following this decline, there was a period of recovery during the early 1980s before the stock collapsed in the early 1990s (Fréchet and Schwab 1998) (Figure 2).

For the purpose of this study, Atlantic cod were divided into adults and juveniles, or more accurately, into large and small fish. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These diet changes tend to occur gradually with increasing length, but here we assume that the change occurs at 35 cm for cod (Lilly 1991). Northern Gulf cod of age 4+ generally represent fish ≥ 35 cm of length, at which size cod become more piscivorous and begin to recruit to the commercial fishery.

Input data (biomass, production, consumption, and catch) used in modelling and estimated fluxes for small and large cod for each period are summarized in Tables 2 and 3. Several scenarios were tested for 1985–1987. Here, we used the estimates from the most realistic solution, the "misreporting solution" that included misreported catches of large cod (Savenkoff et al. 2004b). In this solution, the mean catches of large cod have been increased by 45%, a level consistent with estimates of misreported cod catches in the northern Gulf in the mid-1980s (Savenkoff et al. 2004b). Some values were slightly different from data published in previous technical reports (Morissette et al. 2003, Savenkoff et al. 2004a, Savenkoff et al. 2005) due to model updates.

Catch (Tables 2 and 3)

Since it was assumed that small cod are not recruited to the fishery, and information on by-catch was not available for the northern Gulf area, catch in the model was set to zero for this group. Landings for large cod (age 4+) in NAFO divisions 3Pn4RS are available for each time period (Fréchet et al. 2003, NAFO 2003). Landings from 3Pn, an area at the mouth of the Gulf of St. Lawrence, were included in the model since cod from this area are considered to be part of the stock. In the northern Gulf, the mean annual total catch was 79,217 t or 0.76 t km^{-2} yr^{-1} (SD = 0.11 t km^{-2} yr^{-1}; range: 0.64-0.85 t km^{-2} yr^{-1}) for 1985–1987, 267 t or 0.003 t km^{-2} yr^{-1} (SD = 0.001 t km^{-2} yr^{-1}; range: 0.001-0.004 t km^{-2} yr^{-1}) for 1994–1996, and 6,750 t or 0.065 t km^{-2} yr^{-1} (SD = 0.004 t km^{-2} yr^{-1}; range: 0.062-0.069 t km^{-2} yr^{-1}) for 2000–2002. Even though there is little documented evidence, undeclared catches (non-reported landings and discards at sea) were believed to have been important during the winter otter trawl fishery that occurred during the 1980s (Fréchet 1991). These were mostly age 4 and 5 fish. In the misreporting solution presented here, the fishery catch (1.10 t km^{-2} y^{-1}) of large cod represented a 45% increase in the mean catch value initially used (0.76 t km^{-2} y^{-1}) in the normal solution (Savenkoff et al. 2004b). The 1994–1996 period corresponds to the first moratorium (cessation of directed fishing) on cod fishing. There was no directed cod fishery during these years. In the absence of information for this

species, it was assumed that there were no discards or by-catch. The modelling catch estimates were 1.11, 0.003, and 0.069 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively.

Biomass (Tables 2 and 3)

The biomass of large cod was based on virtual population analysis estimates of cod biomass at the beginning of the year for area 3Pn4RS (Fréchet et al. 2003). Average annual biomass estimates for small cod were 170,545 t or 1.64 t km^{-2} (SD = 0.47 t km^{-2}) for 1985–1987, 6,269 t or 0.06 t km^{-2} (SD = 0.02 t km^{-2}) for 1994–1996, and 12,994 t or 0.12 t km^{-2} (SD = 0.04 t km^{-2}) for 2000–2002. Average annual biomass estimates for large cod were 407,868 t or 3.93 t km^{-2} (SD = 0.81 t km^{-2}) for 1985–1987, 27,803 t or 0.27 t km^{-2} (SD = 0.01 t km^{-2}) for 1994–1996, and 67,244 t or 0.61 t km^{-2} (SD = 0.07 t km^{-2}) for 2000–2002.

Production (Tables 2 and 3)

For small cod, production was assumed to be equivalent to biomass multiplied by natural mortality (M), plus catch ([B x M] + C) (Allen 1971). Natural mortality for small cod was assumed to be 0.6 yr^{-1}, while catch estimates of small cod were assumed to be zero. Mohn and Bowen (1996) used natural mortality values of 1.0, 0.8, 0.6, and 0.4 for cod ages 1 to 4, respectively, in the eastern Scotian Shelf. Using the minimum and maximum biomass values for small cod, we estimated a production range of 0.67 to 1.21 t km^{-2} yr^{-1} (mean: 0.99 ± 0.38 t km^{-2} yr^{-1}) for 1985–1987, 0.01 to 0.06 t km^{-2} yr^{-1} (mean: 0.03 ± 0.04 t km^{-2} yr^{-1}) for 1994–1996, and 0.05 to 0.09 t km^{-2} yr^{-1} (mean: 0.07 ± 0.02 t km^{-2} yr^{-1}) for 2000–2002. The modelling production estimates for small cod were 0.79, 0.06, and 0.08 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively.

The production to biomass ratio (P/B) of large cod was estimated by a catch-curve analysis of groundfish survey data from NAFO divisions 4RS for each time period. The estimate of total mortality was determined from the slope of the regression line fitted to the downward side of the catch curve (Sinclair 2001). The instantaneous rate was then converted into an annual mortality rate ($A = 1 - e^{-Z}$, where Z is the instantaneous mortality rate according to Ricker 1980) (A = 0.76, 0.47, and 0.65 yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively). Since we assume a steady state (no year-to-year change in biomass), total mortality A is equal to the P/B ratio of cod for each period (Allen 1971). When the biomass values were used for each time period, we obtained an annual production estimate of 2.97 ± 0.15 t km^{-2} yr^{-1} (range: 2.86–3.08 t km^{-2} yr^{-1}) for 1985–1987, 0.17 ± 0.03 t km^{-2} yr^{-1} (range: 0.14–0.21 t km^{-2} yr^{-1}) for 1994–1996, and 0.40 ± 0.04 t km^{-2} yr^{-1} (range: 0.35–0.44 t km^{-2} yr^{-1}) for 2000–2002. Production was also estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality for large cod was assumed to be 0.20 yr^{-1} for 1985–1987 (Fréchet and Gagnon 1993), 0.33 yr^{-1} for 1994–1996 (Swain and Castonguay 2000), 0.33 yr^{-1} for 2000 (Swain and Castonguay 2000), and 0.20 yr^{-1} for 2001–2002 (Fréchet et al. 2005). We obtained an annual production of 1.55 ± 0.35 t km^{-2} yr^{-1} (range: 1.24–1.73 t km^{-2} yr^{-1}) for 1985–1987, 0.091 ± 0.003 t km^{-2} yr^{-1} (range: 0.075–0.093 t km^{-2} yr^{-1}) for 1994–1996, and 0.22 ± 0.06 t km^{-2} yr^{-1} (range: 0.17–0.29 t km^{-2} yr^{-1}) for 2000–2002. Combining the two methods resulted in a production range of 1.24 to 3.08 t km^{-2} yr^{-1} for 1985–1987, 0.08 to 0.21 t km^{-2} yr^{-1} for 1994–1996, and 0.17 to 0.44 t km^{-2} yr^{-1} for 2000–2002. The

modelling production estimates for large cod were 1.75, 0.08, and 0.22 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively.

Consumption (Tables 2 and 3)

For 1985–1987 and 1994–1996, four studies were used to estimate the annual food consumption to biomass ratio (Q/B) of small cod extrapolated from food intake measurements (daily or yearly consumption) and body mass or biomass of fish under study. This approach yielded Q/B ratios of 3.25 yr^{-1} (Waiwood et al. 1980), 7.27 yr^{-1} (Daan 1973), 10.73 yr^{-1} (Hawkins et al. 1985), and 2.56 yr^{-1} (Grundwald and Koster 1994). The Q/B ratios for small cod thus varied between 2.56 and 10.73 yr^{-1}. When the biomass values were used for these two time periods, we obtained consumption ranges of 4.21 to 17.63 t km^{-2} yr^{-1} for 1985–1987 and 0.04 to 0.63 t km^{-2} yr^{-1} for 1994–1996. For 2000–2002, we decided to use only the Q/B ratios estimated in the study area more comparable to the northern Gulf (southwestern Gulf of St. Lawrence: 3.25 yr^{-1} in Waiwood et al. 1980; west Greenland waters: 2.56 yr^{-1} in Grundwald and Koster 1994). This improvement decreased the potential consumption values used in modelling, but it was interesting to note that the inverse modelling estimates were already closer the lower consumption constraints for each time period (Table 2). Based on the mean production for each time period and the minimum and maximum gross growth efficiency limits (GE, the ratio of production to consumption, 10–30%; Christensen and Pauly 1992), we obtained consumption ranges of 3.29 to 9.86 t km^{-2} yr^{-1} for 1985–1987, 0.07 to 0.20 t km^{-2} yr^{-1} for 1994–1996, and 0.24 to 0.71 t km^{-2} yr^{-1} for 2000–2002. Assuming that this species would eat at least as much food as its biomass per year ($Q/B \geq 1$), the resulting lower and upper consumption limits were 3.29 and 17.63 t km^{-2} yr^{-1} for 1985–1987, 0.06 (instead of 0.04) and 0.63 t km^{-2} yr^{-1} for 1994–1996, and 0.20 and 0.71 t km^{-2} yr^{-1} for 2000–2002. The modelling production estimates for small cod were 3.34, 0.26, and 0.39 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively.

A range of Q/B values was used to estimate the mean Q/B ratio for large cod. For 1985–1987 and 1994–1996, these values were based on different studies of food consumption by cod populations of other regions (Palomares and Pauly 1989; Pauly 1989) as well as in the Gulf of St. Lawrence (Waiwood et al. 1980). The Q/B ratios for large cod varied between 1.41 (north of Norway; Pauly 1989, Froese and Pauly 2002) and 4.55 yr^{-1} (Scotland; Pauly 1989, Froese and Pauly 2002) (see Savenkoff et al. 2004a for all the values and references). When the biomass values were used for these two time periods, we obtained consumption ranges of 5.54 to 17.88 t km^{-2} yr^{-1} for 1985–1987 and 0.37 to 1.24 t km^{-2} yr^{-1} for 1994–1996. For 2000–2002, we decided to use only the Q/B ratios estimated for the northwest Atlantic (Q/B = 3.43 yr^{-1}; Pauly 1989, Froese and Pauly 2002) as well as in the Gulf of St. Lawrence (Q/B = 1.96 yr^{-1}; Waiwood et al. 1980). The Q/B ratios for large cod varied between 1.96 and 3.43 yr^{-1}, corresponding to a consumption range between 1.06 and 2.31 t km^{-2} yr^{-1}. Once again, we noted that the inverse modelling estimates were already closer the lower consumption constraints for each time period before decreasing the potential consumption values used in modelling (Table 3). Based on the mean production for each time period and the minimum and maximum gross growth efficiency limits (GE, the ratio of production to consumption, 10–30%; Christensen and Pauly 1992), we obtained consumption ranges of 7.71 to 23.12 t km^{-2} yr^{-1} for 1985–1987, 0.38 to 1.13 t km^{-2} yr^{-1} for 1994–1996, and 1.06 to 3.27 t km^{-2} yr^{-1} for 2000–2002. The resulting lower and upper consumption limits were 5.54 and 23.12 t km^{-2} yr^{-1} for 1985–1987, 0.37 and 1.24 t km^{-2} yr^{-1} for

1994–1996, and 1.06 and 3.27 t km^{-2} yr^{-1} for 2000–2002. The modelling production estimates for large cod were 7.23, 0.37, and 1.06 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively.

Diet composition (Tables 4 and 5)

For 1985–1987, we used stomach content data available from NAFO zones 4RS for spring (April-June), summer (July-November), and winter (December-March) of 1983–1988 (D. Chabot, unpublished data). Sampling was length-stratified and covered the inshore and offshore zones for all seasons. In winter, inshore sampling was reduced due to ice cover over most of the northern Gulf of St. Lawrence. Information on empty stomachs is unavailable for this database. Sample sizes for spring, summer, and winter were 401, 310, and 1463, respectively, for large cod and 50, 35, and 212 for small cod. Although cod forage most intensively during the summer (fullness index, excluding empty stomachs, was 1.93, 2.38, and 1.51 for spring, summer, and winter in large cod and 1.56, 3.03, and 1.72 in small cod), most samples (67% of large cod, 71% of small cod) were collected during winter. Therefore, to estimate a diet representative of the entire year, average diets were calculated for each season (in % mass) and then averaged into a final diet using the product "fullness index x season duration (in months)" as a weighting factor. Cod stomach content data were also available for the same region in the summer and winter of 1978–1979 (D. Chabot, unpublished data). This second sample was analyzed in the same manner except that empty stomachs were included in the analysis, as this provides in a better estimate of seasonal fluctuations in stomach fullness. Sample sizes for summer and winter, respectively, were 323 and 634 for large cod and 56 and 154 for small cod. Seasonal values of stomach fullness in large cod were 0.87 and 0.31 in summer and winter, respectively. For small cod, stomach fullness was 0.59 and 0.55 in summer and winter, respectively. These two diets were used as constraints in inverse modelling. For large cod, we also used the study of Minet and Perodou (1978) conducted on cod from the Gulf of St. Lawrence. Overall, the most important prey items of small cod were large zooplankton, capelin, and shrimp (90.6%) (Table 4). The most important prey items of large cod, in percent mass of stomach content, were capelin, piscivorous small pelagics, redfish, and large zooplankton, which together accounted for 68.5% of the diet (Table 5).

For 1994–1996, we used stomach content data available from NAFO divisions 4RS for spring (April-June), summer (July-November), and winter (December-March) from 1993 to 2002 (D. Chabot, unpublished data). We divided the data into two periods: (1) 1994–1996, which represents the sampling period of the mid-1990 model, and (2) 1993 and 1997–2002, hereafter termed the "other-years period." These two periods included samples from large cod for spring, summer, and winter. For small cod, data for the three seasons were available for 1994–1996 while only summer samples were available for the other years. Sampling was length-stratified and covered inshore and offshore zones for all seasons. In winter, inshore sampling was reduced due to ice cover. To estimate a diet representative of the entire year, average diets were calculated for each season (in % mass) and then averaged into a final diet using the product "fullness index x season duration (in months)" as a weighting factor. Empty stomachs were included in the analysis for a better estimate of seasonal fluctuations in stomach fullness. Sample sizes for spring, summer, and winter during the 1994–1996 period were 1137, 4364, and 1510 for large cod and 820, 683, and 708 for small cod, respectively. The fullness indices, including

empty stomachs, were 1.12, 2.10, and 0.24 for spring, summer, and winter in large cod and 4.06, 1.55, and 0.48 in small cod. Sample sizes for spring, summer, and winter during the other-years period were 905, 7409, and 23 for large cod, and the fullness indices, including empty stomachs, were 0.25, 1.62, and 0.60. For small cod, sample size for summer during the other-years period was 2659 and the fullness index, including empty stomachs, was 1.47. These two diets were used as constraints in inverse modelling. Overall, the most important prey items of small cod were shrimp, capelin, and large zooplankton (89.5%; Table 4). The most important prey items of large cod, in percent mass of stomach content, were capelin, large zooplankton, crabs, and planktivorous small pelagics (74.8% of the diet; Table 5).

For 2000–2002, we used stomach content data available for the large and small cod groups from NAFO divisions 4RS from 2000 to 2002 (D. Chabot, unpublished data). The number of stomachs sampled for 2000, 2001, and 2002 were 570, 513, and 287 for large cod and 299, 274, and 99 for small cod, respectively. The fullness indices, including empty stomachs, were 0.95, 1.38, and 1.41 for 2000, 2001, and 2002 in large cod and 0.86, 1.10, and 1.73 in small cod. We used the upper and lower limits of the overall proportion of each prey item by mass as constraints in inverse modelling for the two diet compositions. Overall, the most important prey items of small cod were large zooplankton, shrimp, capelin, and planktivorous small pelagics (94.5% of the diet; Table 4). The most important prey items of large cod, in percent mass of stomach content, were large zooplankton, shrimp, planktivorous small pelagics, and American plaice (68.8% of the diet; Table 5).

RESULTS

Main prey groups consumed by small (< 35 cm) cod

Small cod consumed nineteen prey groups for each period, but their main prey (> 5% of the diet) included only three to four groups (Figure 3). For the mid-1980s, the most important prey items of small cod were large zooplankton (59%), capelin *Mallotus villosus* (21%), and shrimp (mainly *Pandalus borealis*; 10%) (Figure 3). Large zooplankton are organisms and species greater than 5 mm in length and include euphausiids (mainly *Thysanoessa raschii, T. inermis*, and *Meganyctiphanes norvegica)*, chaetognaths (mainly *Sagitta elegans*), hyperiid amphipods (mainly *Themisto libellula, Parathemisto abyssorum*, and *P. gaudichaudii*), jellyfish (cnidarians and ctenophores), mysids (mainly *Boreomysis arctica*), tunicates, and ichthyoplankton. Of these, *T. libellula* was by far the most important in the small cod diet. Small demersal feeders (sculpins *Myoxocephalus* spp., cunner *Tautogolabrus adspersus*, ocean pout *Macrozoarces americanus*) accounted for 4.9% of the diet. Fish prey was made up 27% of the diet composition of small cod. A decrease in consumption by small cod was estimated by the models from the mid-1980s to the mid-1990s (from 3.3 ± 0.2 to 0.3 ± 0.1 t km^{-2} yr^{-1}; Figure 3) in relation to the decrease in small cod biomass (Table 2).

For the mid-1990s, capelin (32%), shrimp (32%), and large zooplankton (28%) were the main prey species (Figure 3). Fish prey made up 37% of the diet composition.

Small cod consumption was similar from the mid-1990s to the early 2000s (0.4 ± 0.2 t km^{-2} yr^{-1}; Figure 3). For the early 2000s, the most important prey items of small cod were large zooplankton (56%), shrimp (20%), and planktivorous small pelagic feeders (mainly Atlantic herring *Clupea harengus*; 13%) (Figure 3). Fish prey accounted for 19% of the diet.

Main prey groups consumed by large (> 35 cm) cod

Large cod consumed twenty prey groups for each period, but their main prey (> 5% of the diet) included only three to six groups (Figure 4). The most important prey items of large cod were capelin (59%), redfish (14%), and large zooplankton (6%). Small cod accounted for 4.8% of the diet. Fish species made up 86% of the large cod diet. Large cod consumption decreased from the mid-1980s to the mid-1990s (from 7.2 ± 2.7 to 0.4 ± 0.0 t km^{-2} yr^{-1}; Figure 4) concurrent with the decrease in large cod biomass (Table 3).

For the mid-1990s, capelin (40%) was the main prey, followed by small crabs (16%) and large zooplankton (15%) (Figure 4). The proportion of shrimp (from 2% to 9%) and planktivorous small pelagics (from 2% to 7%) in the diet composition of large cod increased while the proportion of redfish decreased (from 14% to 2%; Figure 4). The proportion of fish species in the diet composition of large cod decreased to 59%.

Large cod consumption increased from the mid-1990s to the early 2000s (from 0.4 ± 0.0 to 1.1 ± 0.1 t km^{-2} yr^{-1}; Figure 4). For the early 2000s, the most important prey items of large cod were large zooplankton (44%), shrimp (17%), and planktivorous small pelagics (11%) (Figure 4). American plaice *Hippoglossoides platessoides*, capelin, and small crabs accounted for 9%, 7%, and 5%, respectively, of the diet. The overall proportion of fish species in the diet composition of large cod was 32%.

Role played by cod in the northern Gulf ecosystem

During the mid-1980s, large cod were the main predators of fish prey species (Figure 5). After large cod, redfish, capelin (via cannibalism), and small cod were the most important predators of fish. During the mid-1990s, the net decrease in biomass of the demersal species and the ensuing drop in predation coincided with an increase in marine mammal predation. Cetaceans and seals became the main predators on fish. Predation by marine mammals on fish increased from the mid-1980s to early 2000s (from 1.5 ± 0.2 to 3.1 ± 0.7 t km^{-2} yr^{-1}) while predation by large fish on fish decreased (from 15.9 ± 3.0 to 2.2 ± 0.4 t km^{-2} yr^{-1}). Cetaceans and seals were still the main predators on fish, followed by small Greenland halibut during the early 2000s (Figure 5). With the decrease in their biomasses and the ensuing predation fluxes, large cod were progressively replaced by cetacea and seals as the main predators in the system from the mid-1980s to early 2000s.

When the cod biomass was high during the mid-1980s, small cod were among the main predators on fish in the northern Gulf ecosystem (fourth in rank) (Figure 5). Because of the net decrease in cod biomass, small cod as well as large cod were no longer among the four main predators in the ecosystem for the other time periods.

Main mortality causes on small (< 35 cm) cod

Predation dominated total mortality of small cod (71%; Figure 6) during the mid-1980s. Other mortality causes represented about 29% of total mortality. Small cod were assumed not to be recruited to the fishery during any period. Large cod were the main predators followed by large demersal feeders and harp seals. Annual mortality rates for predation and other mortality causes were estimated at 0.34 and 0.14 yr^{-1}, respectively.

From the mid-1980s to mid-1990s, there was a 14-fold decrease in total mortality of small cod (from 0.79 ± 0.10 to 0.06 ± 0.00 t km^{-2} yr^{-1}, Figure 6). Predation was even more dominant as a source of mortality in the mid-1990s (95% versus 71% during the mid-1980s). Grey seals were the main predators in the mid-1990s, followed by harp seals and large cod. The predation impact of seals increased from 10 to 56% of the total mortality of small cod, even though absolute values decreased from 0.08 ± 0.03 to 0.03 ± 0.00 t km^{-2} yr^{-1} (Figure 6). From the mid-1980s to mid-1990s, seal biomass in the study area nearly doubled while small cod biomass decreased 27-fold. Annual mortality rates for predation and other mortality causes were estimated at 0.89 and 0.05 yr^{-1}, respectively.

Total mortality on small cod increased slightly from the mid-1990s (0.06 ± 0.00 t km^{-2} yr^{-1}) to early 2000s (0.08 ± 0.02 t km^{-2} yr^{-1}). Predation remained the dominant source of mortality in the early 2000s (95%) while the other mortality causes accounted for 5%. Seals and cetacea (mainly Odontoceti) were the main predators of small cod (Figure 6). Predation by large cod accounted for 13% of total mortality. Annual mortality rates for predation and other mortality causes were estimated at 0.65 and 0.04 yr^{-1}, respectively.

Main mortality causes on large (> 35 cm) cod

The main predators of large cod were harp and grey seals during the mid-1980s (Figure 7). However, when all mortality causes were considered, predation represented only 2% of the total mortality on large cod (Figure 7). Fishing, including misreported catches, dominated total mortality (64%), whereas other mortality causes contributed 34%. Annual mortality rates for predation, fishing, and other mortality causes were estimated to be 0.01, 0.28, and 0.15 yr^{-1}, respectively.

There was a 23-fold decrease in total mortality of large cod from the mid-1980s to mid-1990s (from 1.75 ± 0.29 to 0.08 ± 0.01 t km^{-2} yr^{-1}, Figure 7). While predation was a minor source of mortality of large cod in the mid-1980s (2%), severe limitations placed on the commercial fisheries in the mid-1990s meant that predation became the dominant source of mortality (66%). The predation impact of seals increased from 2% to 63% of the total mortality of large cod. However, when expressed as absolute values, seal predation levels showed little change (0.04 ± 0.01 and 0.05 ± 0.01 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively) (Figure 7). During the mid-1990s, grey seals were the main predators followed by harp seals (Figure 7). Fishing mortality (from 1.11 ± 0.06 to 0.003 ± 0.001 t km^{-2} yr^{-1}) and other mortality causes (from 0.60 ± 0.28 to 0.02 ± 0.00 t km^{-2} yr^{-1}) decreased sharply from the mid-1980s to the mid-1990s moratorium period. Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.19, 0.01, and 0.08 yr^{-1}, respectively.

Total mortality on large cod increased from the mid-1990s (0.08 ± 0.01 t km^{-2} yr^{-1}) to early 2000s (0.22 ± 0.01 t km^{-2} yr^{-1}). Although predation, fishing, and other mortality causes all

increased, the most noticeable increase in mortality from the mid-1990s to early 2000s came from fishing (by a factor of 23, from 0.003 ± 0.001 to 0.069 ± 0.003 t km^{-2} yr^{-1}, Figure 7). Predation accounted for 29% of total mortality, whereas other mortality causes and fishing represented 40% and 31% of total mortality, respectively. Grey and harp seals were the main predators of large cod (Figure 7). Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.10, 0.11, and 0.14 yr^{-1}, respectively.

DISCUSSION

The analysis enables us to evaluate the relative impact and interplay of the main mortality causes (fishing, predation, and natural mortality other than predation) on small and large cod in the northern Gulf of St. Lawrence during three time periods that cover the collapse of demersal species and the management regulations that followed. In the northern Gulf, there was a net decrease in total mortality and predation on small and large cod from the mid-1980s to the mid-1990s. Fishing mortality on large cod also decreased over the same time period as the cod fishery in the Gulf was under moratorium. From the mid-1990s to early 2000s, the biomass of both small and large cod doubled. Predation on small cod increased slightly over the same time period (from 0.05 to 0.08 t km^{-2} yr^{-1}) while predation on large cod was similar (0.05–0.06 t km^{-2} yr^{-1}). However, the most noticeable increase in mortality of large cod from the mid-1990s to early 2000s came from fishing.

The reasons for the collapse and lack of recovery of depleted cod fish stocks during and after the moratorium are complex and no single factor can explain all observations. Major changes in the structure and functioning of the northern Gulf ecosystem accompanied the collapse of the large-bodied demersal predators in the late 1980s and early 1990s due to overfishing (Savenkoff et al. submitted). Overfishing removed a large portion of a functional group, large piscivorous fish that has not been replaced 12 years after the cessation of heavy fishing (Rice and Rivard 2003). The result of the disappearance of these (formerly more important) predators left only marine mammals as the top predators of many species during the mid-1990s, and marine mammals and small Greenland halibut during the early 2000s. Hence seals became significant predators of juvenile cod during the mid-1990s and early 2000s. This, as well as predation on adults, may have played a role in the slower-than-expected recovery of cod. However, other factors may also be involved in the slow of recovery of depleted stocks, including low spawning stock biomass, low recruitment rate, and predation by pelagic fish on different life stages of cod.

The spawning stock biomass (SSB) declined from almost 400,000 t in 1983 to a minimum of 10,000 t in 1994 (start of the first moratorium; Figure 8a) (Fréchet et al. 2005). It slowly increased to around 40,000 t until 1997, when the fishery reopened, and has remained at that level since (Fréchet et al. 2005). Also, the recruitment rate (age 3 biomass/SSB) declined from 1974 to 1989 and peaked in 1994 (the year with the smallest SSB in the time series) and has remained stable at low levels since1999 (Figure 8b). The good survival of the 1993 year class has provided evidence that natural mortality has declined recently. This year class has supported the fishery for many years. Nevertheless, recent recruitment is still very low. In fact, Swain and Castonguay (2000) suggested that the loss of a spawning component and/or the reduced area occupied by spawners may be preventing recovery in the northern Gulf while the recruitment rate does not appear to be lower than normal for the northern cod stock.

Another hypothesis for the lack of recovery by cod following the fishing moratorium is that predation by pelagic fish on early life stages may have a strong negative effect on cod recruitment success. In the southern Gulf of St. Lawrence, Swain and Sinclair (2000) presented evidence that high pelagic fish biomass had a strong negative effect on cod recruitment success. Walters and Kitchell (2001) proposed that the success of many commercially important fish stocks depends on "cultivation" effects in which the adults crop down forage fish that are predators or competitors of their early life history stages. Hence, when adult abundance is severely depleted by fishing, cod prerecruit survival would be affected by top-down control by pelagic fish through predation on eggs and larvae. Similar effects of pelagic fish on cod recruitment have been proposed for the Baltic Sea (Köster and Möllmann 2000), the North Sea (Daan et al. 1994), and the Grand Banks (Paz and Larrañeta 1992). However, the available data showed few cod eggs or larvae in the diet of pelagic fish in the southern Gulf of St. Lawrence (Darbyson et al. 2003), but fish larvae are digested very quickly and cod eggs and larvae were not abundant during the survey period. Predation by pelagic species on small cod, including eggs and larvae, was weakly constrained in the models (at most 0.3% of the diet of pelagic species). It is therefore possible that the impact of pelagic fish on small cod was underestimated by our models. When capelin biomass was excluded from the calculation (capelin biomass was poorly estimated by the trawl survey and there are no estimates of absolute biomass), the biomass ratio of pelagic to demersal fish species increased from 0.36 in the mid-1980s (pelagic and demersal biomasses: 7.9 and 21.8 t km^{-2}, respectively) to 0.86 in the early 2000s (pelagic and demersal biomasses: 4.1 and 4.8 t km^{-2}, respectively). This finding shows the importance of the pelagic component in the northern Gulf.

Population models of exploited fish stocks include a cannibalism component that will tend to depress recruitment at high stock size (Hilborn and Walters 1992). Cannibalism appeared to be an important source of mortality on small cod in the northern Gulf. Cannibalism by large cod was the main source of mortality of small cod (44%) during the mid-1980s and still had a significant effect during the mid-1990s and early 2000s (25% and 13% of total mortality of small cod, respectively), even though small cod constituted a minor component of the diet of large cod (at most 6%). A larger impact of cannibalism during periods of high juvenile and adult abundance was also reported by Neuenfeldt and Köster (2000) for the Baltic Sea cod stock.

Other possible explanations for the high other mortality of large cod in our models include underestimation of predation mortality or increases in starvation and disease linked to poor environmental conditions.

It seems unlikely that our models underestimate predation on cod by seals, their main predators in our models. The proportion of cod in the diet was constrained within the minimum and maximum percentage observed in any single diet sample obtained from different diet studies conducted in the St. Lawrence Estuary, the northern Gulf, and other waters of the Northwest Atlantic (Morissette et al. 2003, Savenkoff et al. 2004a, Savenkoff et al. 2005). The seal diets in our model solutions contained high proportions of cod. These proportions, particularly those eaten by grey seals (between 17.5% and 26.0%), are very high compared to findings in other areas (6% in Hammill and Stenson 2002). The high other mortality of large cod may be partly attributable to underestimated predation by cetaceans (Folkow et al. 2000) or other potential predators such as large sharks. Unfortunately, information on both groups is lacking. To account for the other mortality, however, large cod would have to represent 21.0% of the biomass eaten by all cetaceans combined for the early 2000s (versus 2.7% used as upper limit constraint).

Other potential sources of mortality include starvation, disease, parasites, and toxic contaminants. The Gulf of St. Lawrence has been experiencing below-normal water temperatures in the cold intermediate layer since the mid-1980s (DFO 2004). Dutil and Brander (2003) showed that during this period, North Atlantic cod stocks have become less productive and hence less resilient, i.e., less able to resist and respond to perturbations, whether man-made or environmental. Stocks living in the northern portion of the distribution range, such as the northern Gulf stock, are unable to quickly produce new biomass. As a result, stock rebuilding is expected to take longer than would be predicted for other stocks living in more favourable environments, particularly if exploited under adverse environmental conditions of long duration (Dutil and Brander 2003). Supporting the idea of an adverse effect of cold temperatures on cod survival, poor condition (energy reserves) has been documented in the northern Gulf cod between the mid-1980s and the mid-1990s (Lambert and Dutil 1997, Dutil and Lambert 2000, Dutil et al. 2003). Starvation and disease linked to poor environmental conditions could be other possible explanations for the high mortality by other causes of large cod in our models, but mainly in the late 1980s and early 1990s. It is also possible that the model is failing to capture a source of mortality that occurs outside the model area, or that the biomass or productivity in the area has been incorrectly estimated.

CONCLUSION

Ecosystem models could become powerful new tools for fishery management. The results already provide valuable information on the relative impact of fishing on exploited species and on the effects of the major mortality causes (fishing, predation, and natural mortality other than predation) on the fish and invertebrate communities. Such models provide a useful starting point to frame hypotheses about the ecosystem to identify data gaps and to show where the uncertainties in the food web occur that could be examined in future studies. Progress is still needed to refine our understanding of the structure of ecosystems in the Gulf of St. Lawrence as well as in other areas of the world. Information on the impact of fishing and predation on cod stocks in the Gulf of St. Lawrence has to continue to be investigated to improve management practices.

Modelling of large marine ecosystems is still in its infancy. Our current models, even with 30 compartments, still represent simplifications of the trophic interactions in the northern Gulf of St. Lawrence. However, the changes that occurred in the northern Gulf over the past 20 years were driven by human exploitation of selected species and would largely qualify as a fishery-induced regime shift. A return to the historical equilibrium is expected to take a long time, if it happens at all, especially considering the continued fishing on cod at current low levels of abundance (fishing still represented 32% of total mortality on large cod during the early 2000s).

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Table 1. Functional groups used in modelling in the northern Gulf of St. Lawrence for each time period.

Group name	Main species
Cetaceans[a]	Mysticeti (baleen whales): *Balaenoptera physalus*, *Balaenoptera acutorostrata*, *Megaptera novaeangliae*
	Odontoceti (toothed whales): *Lagenorhynchus acutus*, *L. albirostris*, *Phocoena phocoena*
Harp seals[b]	*Pagophilus groenlandicus*
Hooded seals[b]	*Cystophora cristata*
Grey seals[c]	*Halichoerus grypus*
Harbour seals[c]	*Phoca vitulina*
Seabirds	*Phalacrocorax carbo*, *P. auritus*, *Larus delawarensis*, *L. argentatus*, *L. marinus*, *Sterna hirundo*, *S. paradisaea*, *Cepphus grylle*, *Oceanodroma leucorhoa*, *Morus bassanus*, *Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)	*Reinhardtius hippoglossoides*
American plaice	*Hippoglossoides platessoides*
Flounders	*Limanda ferruginea*, *Glyptocephalus cynoglossus*, *Pseudopleuronectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes mentella*, *Sebastes fasciatus*
Large demersal feeders	*Urophycis tenuis*, *Melanogrammus aeglefinus*, *Centroscyllium fabricii*, *Anarhichas* spp., *Cyclopterus lumpus*, *Lycodes* spp., Macrouridae, Zoarcidae, *Lophius americanus*, *Hippoglossus hippoglossus*
Small demersal feeders	*Myoxocephalus* spp., *Tautogolabrus adspersus*, *Macrozoarces americanus*, juvenile large demersals
Capelin	*Mallotus villosus*
Sand lance[d]	*Ammodytes* spp.
Arctic cod[e]	*Boreogadus saida*

Table 1. Cont.

Group name	Main species
Large pelagic feeders	*Squalus acanthias*, *Pollachius virens*, *Merluccius bilinearis*
Piscivorous small pelagic feeders	*Scomber scombrus*, piscivorous myctophids and other mesopelagics, *Illex illecebrosus*, piscivorous juvenile large pelagics
Planktivorous small pelagic feeders	*Clupea harengus*, planktivorous myctophids and other mesopelagics, *Scomberesox saurus*, *Gonatus* spp., planktivorous juvenile large pelagics
Shrimp[f]	*Pandalus borealis*, *P. montagui*, *Argis dentata*, *Eualus macilentus*, *E. gaimardii*
Crabs[g]	*Chionoecetes opilio*, other non-commercial species (e.g., *Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Strongylocentrotus pallidus*, *Ophiura robusta*
Molluscs	*Mesodesma deauratum*, *Cyrtodaria siliqua*
Polychaetes	*Exogone hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates)

Table 1. Cont.

Group name	Main species
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *C.* spp., *Leptocylindrus minimus*, *Thalassiosira nordenskioeldii*, *T.* spp., *Fragilariopsis* spp., and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, and Prymnesiophytes
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

[a]: Cetaceans were separated into two groups for the early 2000s: the mysticeti (baleen whales) and the odontoceti (toothed whales).
[b]: Harp and hooded seals were grouped in the early 2000s. Hooded seals accounted for 4–5% of this group biomass for each time period.
[c]: Grey and harbour seals were grouped in the early 2000s. Harbour seals accounted for 11–14% of this group biomass for each time period.
[d]: Included in the planktivorous small pelagic feeders in the early 2000s.
[e]: Included in the capelin group in the early 2000s.
[f] Shrimp were separated into large (≥ 22 mm carapace length, CL; mainly female *Pandalus borealis*) and small (< 22 mm CL) shrimp in the early 2000s.
[g]: Crabs were separated into small (≤ 45 mm carapace width, CW) and large (> 45 mm CW) crabs in the early 2000s.

Table 2. Mean, minimum, and maximum values for small cod used in inverse modelling for each time period. Modelling estimates are also shown. Inverse modelling does not provide estimates of biomass. Values used in data equations or as upper and lower limit constraints are indicated in boldface[a].

Parameter	1985–1987	1994–1996	2000–2002
Mean biomass (t km^{-2})	1.64	0.06	0.12
Minimum biomass (t km^{-2})	1.11	0.02	0.08
Maximum biomass (t km^{-2})	2.02	0.06	0.15
Mean production (t km^{-2} yr^{-1})	0.99	0.03	0.07
Minimum production (t km^{-2} yr^{-1})	**0.67**	**0.01**	**0.05**
Maximum production (t km^{-2} yr^{-1})	**1.21**	**0.06**	**0.09**
Estimated production (t km^{-2} yr^{-1})	0.79	0.06	0.08
Mean consumption (t km^{-2} yr^{-1})	10.46	0.35	0.46
Minimum consumption (t km^{-2} yr^{-1})	**3.29**	**0.06**	**0.20**
Maximum consumption (t km^{-2} yr^{-1})	**17.63**	**0.63**	**0.71**
Estimated consumption (t km^{-2} yr^{-1})	3.34	0.26	0.39

[a]: Some of the input data were introduced directly into the models as data equations. The data equations attempt to fix the value of certain flows or combinations of flows. These included mean values (e.g., catch) estimated from field studies and values available only as point estimates (no variance) or with low observed values (e.g., <0.5%) and low uncertainty (e.g., SD < 0.6%). The production and consumption values that were not estimated from local field studies as well as the diet proportions with higher values (e.g., >0.5%) were incorporated as constraints.

Table 3. Mean, minimum, and maximum values for large cod used in inverse modelling for each time period. Modelling estimates are also shown. Inverse modelling does not provide estimates of biomass. Values used in data equations or as upper and lower limit constraints are indicated in boldface[a].

Parameter	1985–1987	1994–1996	2000–2002
Mean catch (t km^{-2} yr^{-1})	**0.76 (1.10)**[b]	**0.003**	**0.065**
Minimum catch (t km^{-2} yr^{-1})	0.64	0.001	0.062
Maximum catch (t km^{-2} yr^{-1})	0.85	0.004	0.069
Estimated catch (t km^{-2} yr^{-1})	1.11	0.003	0.069
Mean biomass (t km^{-2})	3.93	0.27	0.61
Minimum biomass (t km^{-2})	2.99	0.26	0.54
Maximum biomass (t km^{-2})	4.40	0.27	0.67
Mean production (t km^{-2} yr^{-1})	2.31	0.11	0.33
Minimum production (t km^{-2} yr^{-1})	**1.24**	**0.08**	**0.17**
Maximum production (t km^{-2} yr^{-1})	**3.08**	**0.21**	**0.44**
Estimated production (t km^{-2} yr^{-1})	1.75	0.08	0.22
Mean consumption (t km^{-2} yr^{-1})	14.33	0.80	2.17
Minimum consumption (t km^{-2} yr^{-1})	**5.54**	**0.37**	**1.06**
Maximum consumption (t km^{-2} yr^{-1})	**23.12**	**1.24**	**3.27**
Estimated consumption (t km^{-2} yr^{-1})	7.23	0.37	1.06

[a]: Some of the input data were introduced directly into the models as data equations. The data equations attempt to fix the value of certain flows or combinations of flows. These included mean values (e.g., catch) estimated from field studies and values available only as point estimates (no variance) or with low observed values (e.g., <0.5%) and low uncertainty (e.g., SD < 0.6%). The production and consumption values that were not estimated from local field studies as well as the diet proportions with higher values (e.g., >0.5%) were incorporated as constraints.

[b]: In the misreporting solution, the fishing catch (1.10 t km^{-2} y^{-1}) of large cod represented a 45% increase in the mean catch value initially used (0.76 t km^{-2} y^{-1}) in the normal solution.

Table 4. Diet composition of small cod used in modelling for each time period. Est: diet estimates by the inverse model; SD: standard deviation. All values are percentages. Empty cells indicate that a prey item was never found whereas a value of "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	1985–1987					1994–1996					2000–2002				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Small cod	**0.2**	0.2	0.0	0.3	0.2	**0.1**	0.1	0.0	0.2	0.1	**0.0**	0.0	0.0	0.0	0.0
Small Green. halibut	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.1	0.0	0.2	0.0
American plaice	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.1	0.0	0.2	0.0
Flounders	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.1	0.0	0.2	0.0
Skates															
Redfish	**0.0**	0.0	0.0	0.0	0.0	**0.1**	0.2	0.0	0.3	0.1	**0.0**	0.0	0.0	0.0	0.0
Small demersals	5.0	6.6	**0.4**	**9.7**	4.9	1.6	0.8	**1.0**	**2.2**	1.1	2.2	2.4	**1.9**	**5.3**	2.0
Capelin	18.3	3.8	**15.6**	**20.9**	20.7	30.1	4.8	**26.7**	**33.5**	32.0	9.0	9.1	**2.4**	**15.3**	4.3
Pisci. small pelagics	**0.0**	0.0	0.0	0.0	0.0	**0.1**	0.1	0.1	0.1	0.1	**0.0**	0.0	0.0	0.0	0.0
Plank. small pelagics	0.6	0.8	**0.0**	**1.1**	1.1	5.8	2.0	**3.7**	**7.8**	3.9	8.7	13.1	**0.0**	**18.5**	13.0
Shrimp	15.4	8.1	**9.7**	**21.1**	9.9	32.8	7.0	**27.9**	**37.7**	31.7	22.0	10.5	**11.6**	**31.4**	20.1
Crabs	**0.4**	0.4	0.1	0.7	0.4	2.0	0.7	**1.4**	**2.5**	2.0	1.0	1.2	**0.1**	**1.7**	0.1
Echinoderms	**0.1**	0.2	0.0	0.2	0.1	**0.0**	0.0	0.0	0.1	0.0	**0.0**	0.0	0.0	0.0	0.0
Molluscs	**0.1**	0.0	0.1	0.1	0.1	**0.0**	0.0	0.0	0.1	0.0	**0.0**	0.0	0.0	0.0	0.0
Polychaetes	**2.0**	0.5	1.7	2.4	2.0	**0.4**	0.2	0.2	0.5	0.4	**1.0**	1.6	0.0	2.3	2.1
Other bent. inver.	**0.2**	0.2	0.0	0.3	0.2	**0.0**	0.0	0.0	0.1	0.0	**0.0**	0.1	0.0	0.1	0.0
Large zooplankton	56.9	5.9	**52.8**	**61.1**	59.0	26.6	9.7	**19.8**	**33.5**	28.2	54.7	30.1	**38.1**	**80.7**	56.4
Small zooplankton	0.9	0.8	**0.3**	**1.4**	1.4	**0.3**	0.3	0.1	0.5	0.3	1.2	1.8	**0.0**	**2.6**	1.9
Total	100.0		80.6	119.4	100.0	100.0		81.0	119.0	100.0	100.0		54.0	158.6	100.0

Table 5. Diet composition of large cod used in modelling for each time period. Est: diet estimates by the inverse model; SD: standard deviation. All values are percentages. A value of "0.0" indicates that a prey item was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	1985–1987					1994–1996					2000–2002				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Small cod	2.7	2.7	**0.8**	**5.8**	4.8	4.3	0.8	**3.8**	**4.8**	3.8	3.8	3.5	**0.0**	**4.9**	1.0
Small Green. halibut	**0.3**	0.5	0.0	0.8	0.3	**0.4**	0.5	0.0	0.7	0.4	**0.0**	0.0	0.0	0.0	0.0
American plaice	2.9	3.1	**0.0**	**6.2**	2.0	2.3	1.6	**1.1**	**3.4**	2.8	13.0	11.3	**5.4**	**21.4**	9.2
Flounders	1.9	1.0	**1.1**	**3.0**	1.3	1.1	0.9	**0.5**	**1.7**	0.5	5.7	9.1	**0.0**	**12.9**	0.0
Skates	**0.2**	0.2	0.0	0.4	0.2	**0.0**	0.0	0.0	0.1	0.0	**0.0**	0.0	0.0	0.0	0.0
Redfish	11.8	4.3	**8.0**	**16.4**	14.1	**1.7**	0.6	1.3	2.1	1.7	2.0	1.7	**0.2**	**2.6**	0.9
Small demersals	3.6	5.0	**0.0**	**9.2**	0.0	3.3	1.1	**2.4**	**4.1**	2.4	4.0	1.8	**2.9**	**5.4**	2.9
Capelin	32.7	37.6	**4.0**	**80.2**	59.4	34.7	10.8	**26.9**	**42.6**	39.5	4.6	2.9	**4.0**	**8.2**	7.0
Pisci. small pelagics	13.8	23.6	**0.0**	**41.1**	1.5	**0.9**	0.1	0.8	1.0	0.9	**0.1**	0.2	0.0	0.3	0.1
Plank. small pelagics	6.9	4.1	**2.1**	**9.4**	2.1	11.4	5.5	**6.6**	**16.1**	7.0	15.7	15.5	**5.0**	**26.9**	10.9
Shrimp	4.0	1.6	**2.2**	**5.3**	2.2	9.4	4.1	**6.5**	**12.2**	9.0	16.8	5.8	**9.6**	**21.0**	16.6
Crabs	4.2	3.3	**0.4**	**6.3**	0.4	14.1	11.0	**6.3**	**21.8**	15.5	9.7	4.5	**5.0**	**11.5**	5.0
Echinoderms	2.6	2.1	**0.6**	**4.7**	2.8	**1.1**	0.1	1.0	1.1	1.1	**0.5**	0.5	0.1	0.7	0.5
Molluscs	1.0	0.9	**0.4**	**2.0**	1.3	**0.4**	0.4	0.1	0.6	0.4	0.4	0.7	**0.1**	**1.1**	1.0
Polychaetes	1.0	0.9	**0.0**	**1.9**	1.2	**0.1**	0.1	0.1	0.2	0.1	**0.4**	0.3	0.2	0.5	0.4
Other bent. inver.	**0.3**	0.2	0.0	0.5	0.3	**0.1**	0.1	0.0	0.2	0.1	**0.0**	0.0	0.0	0.1	0.0
Large zooplankton	10.3	14.4	**1.2**	**26.9**	5.9	**14.6**	0.5	14.3	15.0	14.6	23.4	23.3	**12.6**	**45.5**	44.5
Small zooplankton	**0.1**	0.1	0.0	0.1	0.1	**0.2**	0.1	0.1	0.3	0.2	**0.0**	0.0	0.0	0.0	0.0
Total	100.0		20.8	220.2	100.0	100.0		72.0	128.0	100.0	100.0		45.0	163.0	100.0

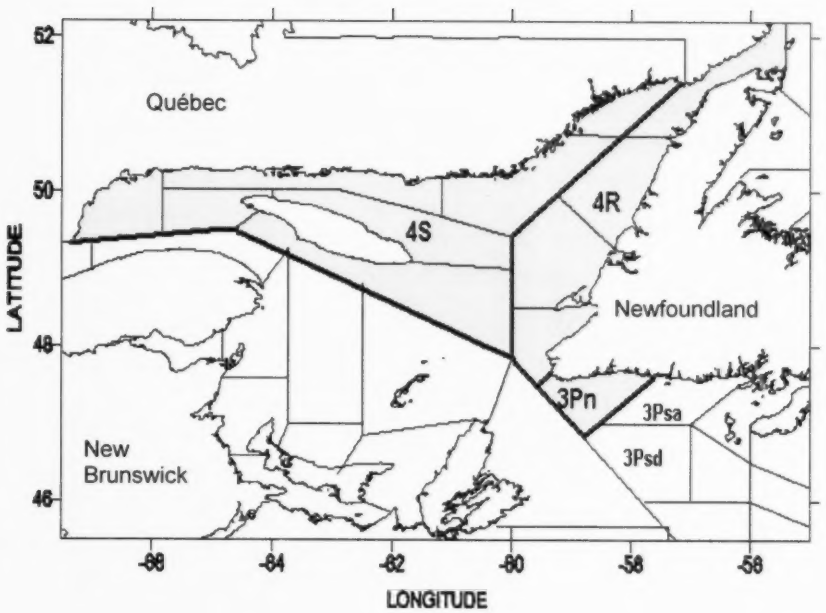

Figure 1. Gulf of St. Lawrence map showing NAFO divisions 4R, 4S, and 3Pn, which constitute the management unit for the northern Gulf of St. Lawrence cod.

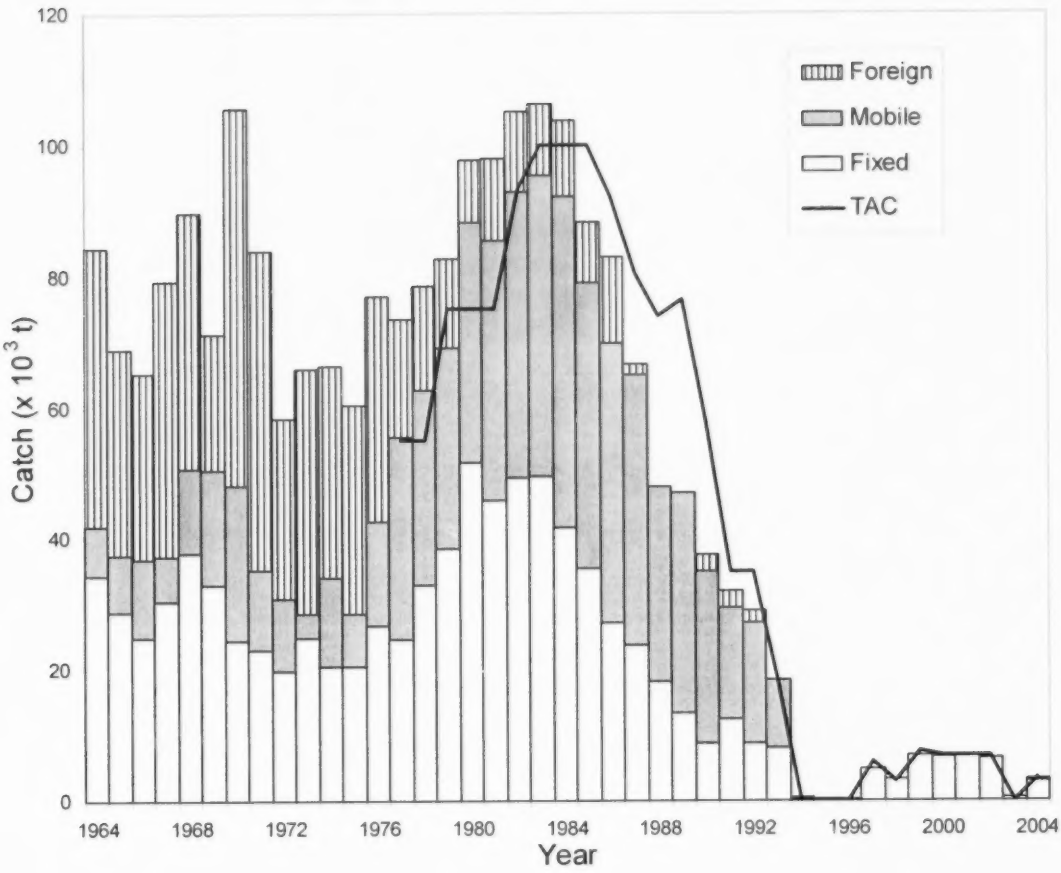

Figure 2. Historical catches and total allowable catch (TAC) for 4RS3Pn cod (from Fréchet et al. 2005). Foreign: catches by countries other than Canada (mostly France, Spain, and Portugal); mobile gears: Canadian catches by Danish seines, pair trawls, and otter trawls (both side and stern); fixed gears: Canadian catches by dory vessels, traps, gillnets, handlines, and longlines.

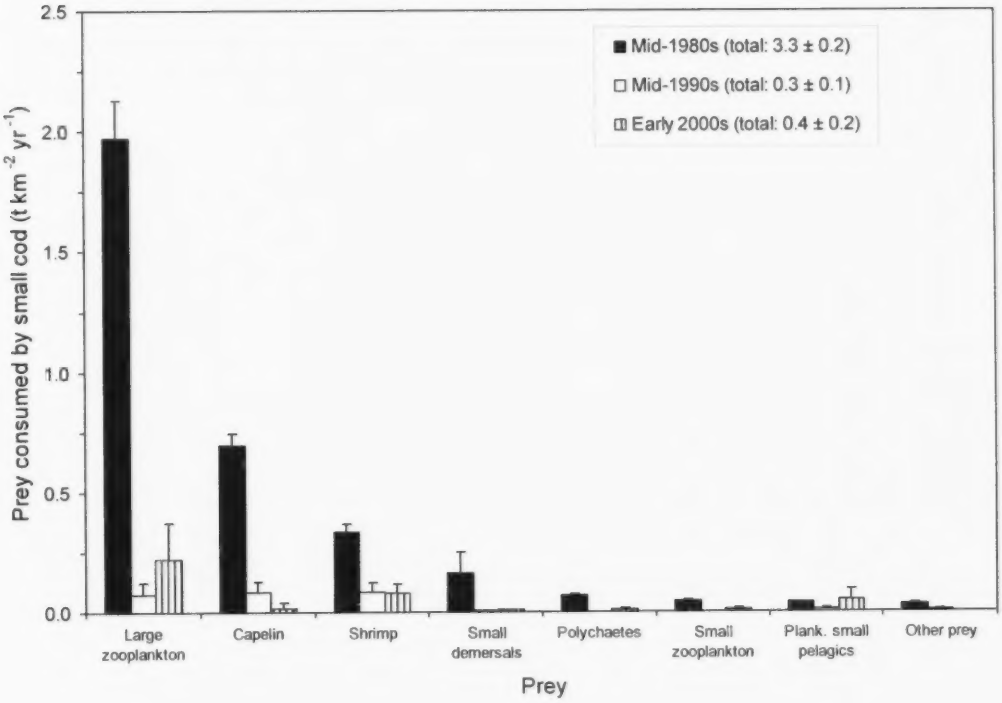

Figure 3. Prey consumed by small (< 35 cm) cod estimated for each time period. Total small cod consumption for each time period (in t km^{-2} yr^{-1}) is shown in the legend. Bars show mean values and SD.

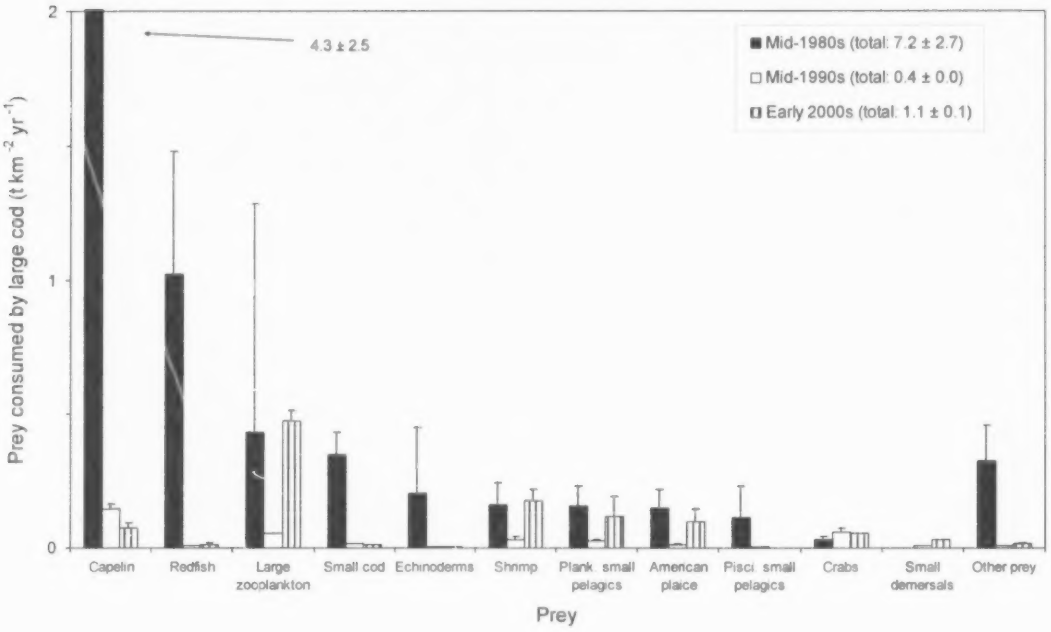

Figure 4. Prey consumed by large (> 35 cm) cod estimated for each time period. Total large cod consumption for each time period (in t km^{-2} yr^{-1}) is shown in the legend. Bars show mean values and SD.

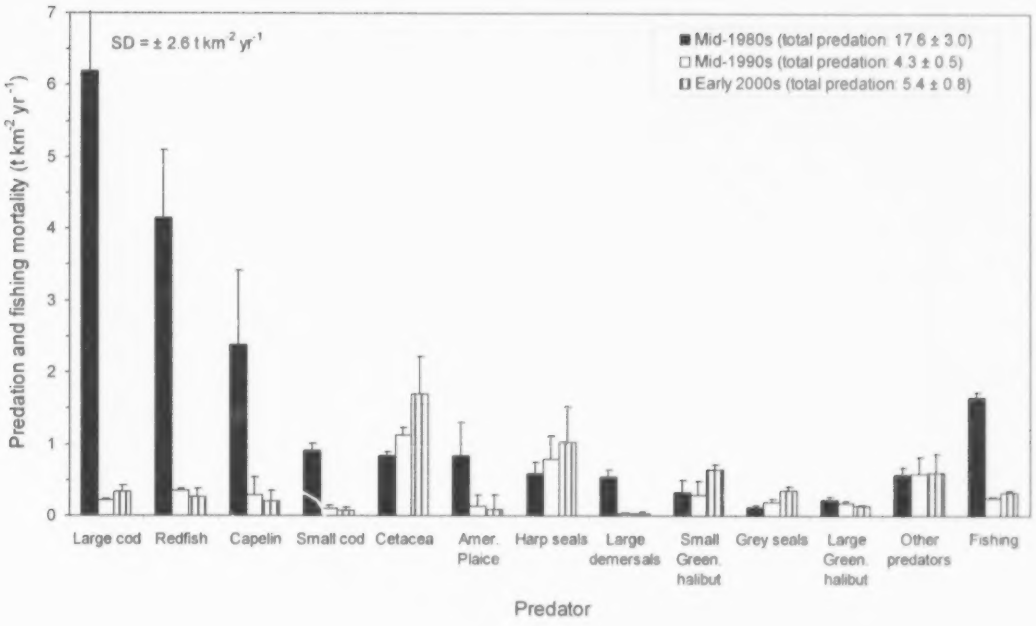

Figure 5. Predation mortality on fish by different groups showing the main predators in the northern Gulf for each time period. For comparison, fishing mortality on fish is also included. The "other predators" group accounted for 3% (seabirds: 0.8%, small demersals: 0.6%, and other species: < 0.4% each) during the mid-1980s, 13% (seabirds: 5.3%, piscivorous small pelagics: 3.3%, small demersals: 2.0%, skates: 1.8%, and other species: < 0.2% each) during the mid-1990s, and 10% (seabirds: 3.5%, piscivorous small pelagics: 2.9%, and other species: < 1.2% each) during the early 2000s. Bars show mean values and SD.

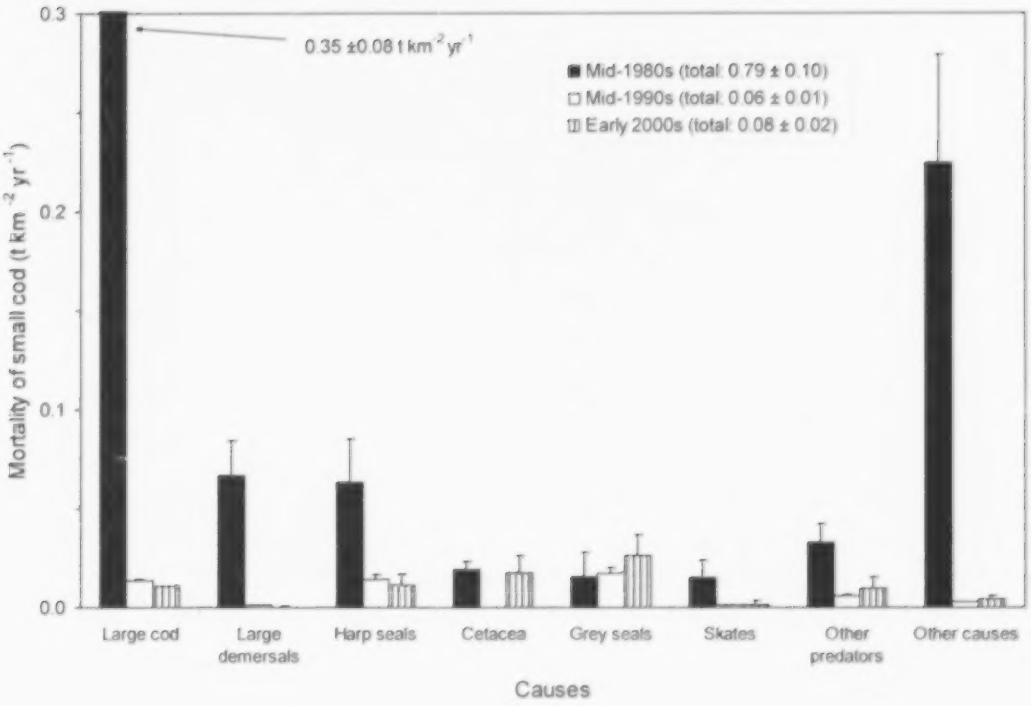

Figure 6. Main mortality causes (predation and natural mortality other than predation, i.e., other causes) for small (< 35 cm) cod estimated for each time period. Bars show mean values and SD.

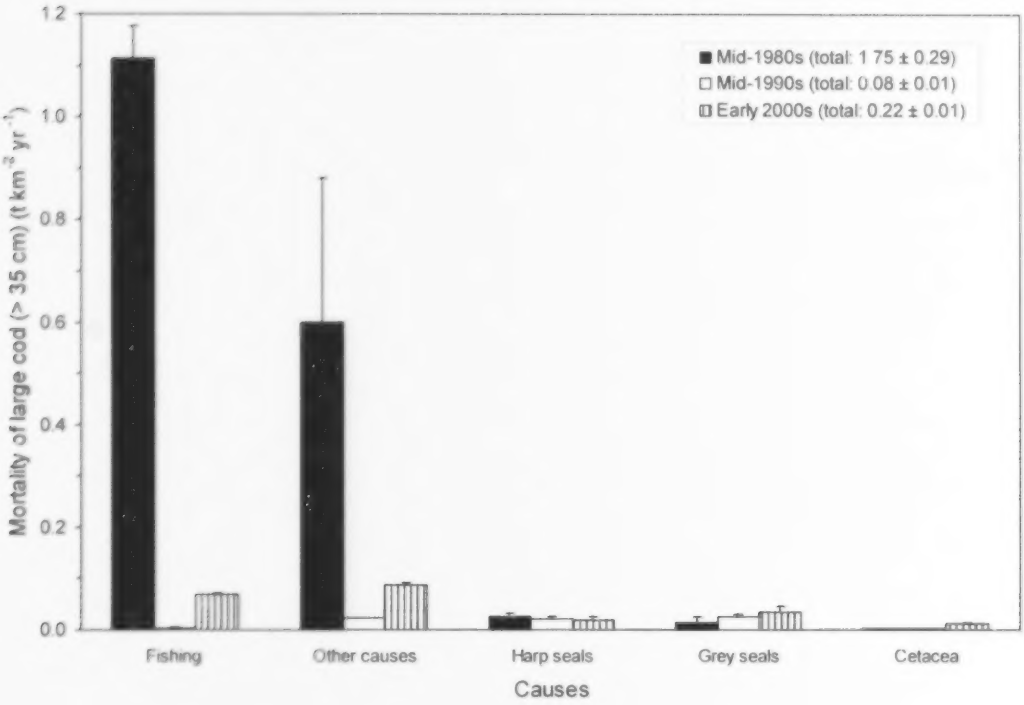

Figure 7. Main mortality causes (fishing, predation, and natural mortality other than predation, i.e., other causes) for large (> 35 cm) cod estimated for each time period. Bars show mean values and SD.

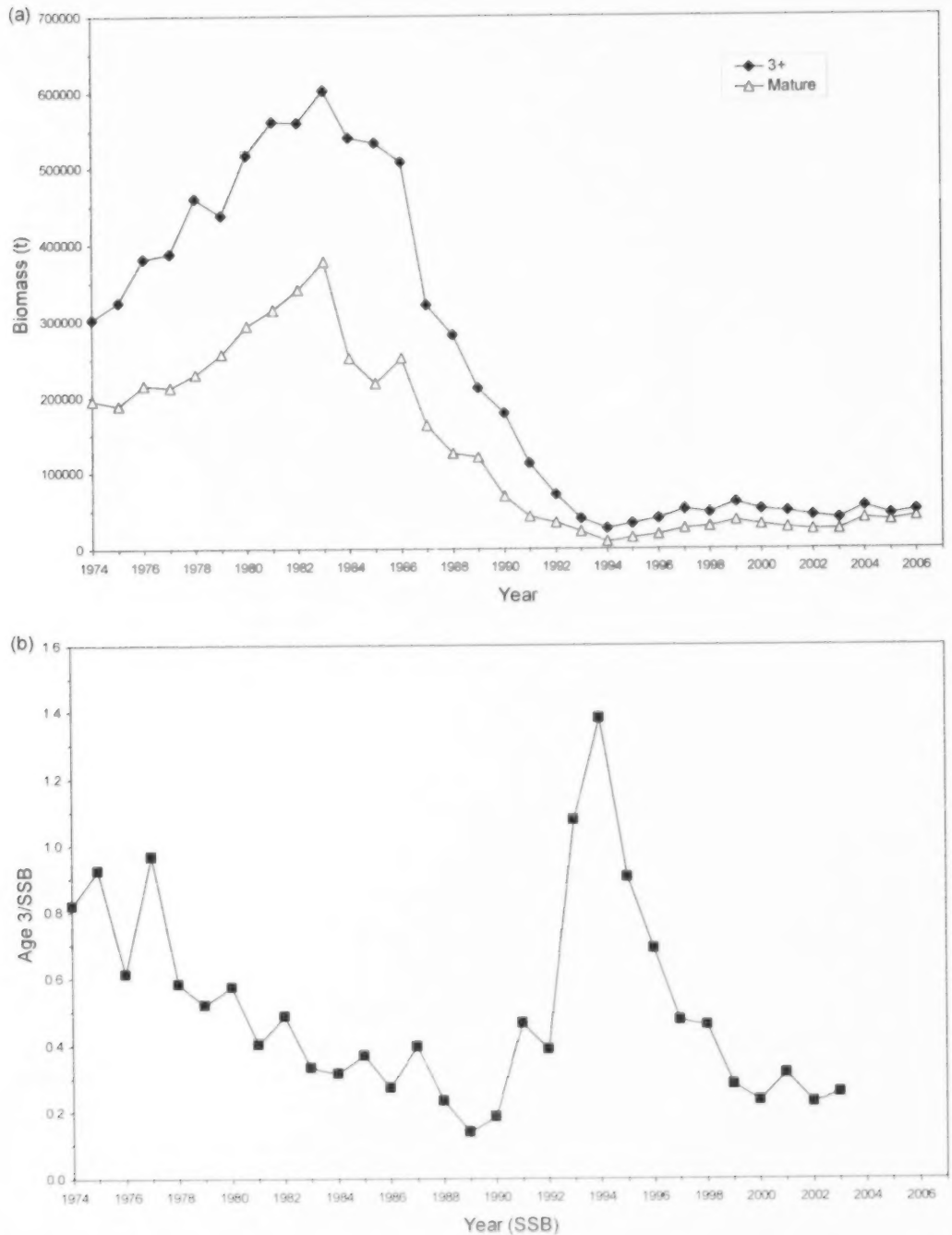

Figure 8. (a) Cod spawning stock biomass (mature; SSB) and total biomass (age 3+) and (b) recruitment rate (age 3 biomass/SSB) by year.